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# Life syndrome of the bryophyte communities as an adaptative pattern in the Mediterranean temporary ponds of Italy

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**Abstract**

An ecological and biological investigation on the bryophyte communities of the Mediterranean temporary ponds was carried out in Italy. Here, the occurrence of a rich set of liverworts is very significant, as several species of *Riccia* characterize the communities from a physiognomical, ecological and syntaxonomical point of view. The moss component is represented only by acrocarpous mosses, e.g. *Archidium alternifolium* and *Pleuridium acuminatum* which play an important phytosociological role. In this study, the bryophyte communities are used to identify a pattern, corresponding to a "functional type" which reflects the correlated response of the bryophyte communities toward the prevalent ecological parameters of the habitat. The individuated functional type assembles life strategy, life form, lifespan, spore size, dispersal strategy, reproduction effort, independently from the taxonomical relationship of the species characterizing the communities. It represents an adaptative pattern of coevolved characters, adopted by the bryophyte communities for the habitat establishment and re-establishment following the seasonal water fluctuations typical of the investigated habitat.

**Keywords:** *Bryophytes, life syndrome, functional type, Mediterranean temporary ponds, Italy*

## Introduction

The Mediterranean temporary ponds are very important wetlands for the survival and conservation of plants, including bryophytes. They comprise a priority habitat according to the Natura 2000 network of the European Union (Nature code 3170*, Habitats Directive 92/43/EC) well represented in the Mediterranean region (Bagella & Caria 2012; Bagella et al. 2013; Minissale & Sciandrello 2016; Caria et al. 2015; etc.). These water bodies, subjected to intermittent and unstable environmental conditions, remain flooded in winter and sometimes spring, allowing the development of a specialized vascular flora mainly composed of Mediterranean therophytic and geophytic species. The vegetation is syntaxonomically referable to the southern amphibious communities of the order *Isoëtetalia durieui* Br.-Bl. 1936 and also to the communities of the *Nanocyperetalia flavescentis* Klika 1935 of the class *Isoëto-Nanojuncetea* Br.-Bl. & Tüxen ex Westhoff, Dijk & Passchier 1946. Apart from natural hydrologic and climatic events, which are the major biological regulatory factors, anthropogenic activities pose serious threats to these habitats, that are extremely vulnerable and must be safeguarded.

The vascular plants, as well as the bryophytes linked to this habitat, are represented by specialized taxa, depending mainly on the flooding/drying regime to complete their life cycle. The ecological features of the habitat cause a selection that allows the establishment of a flora characterized by liverworts, with the prevalence of species of the genera *Riccia*, *Fossombronia*, and mosses, with the prevalence of *Archidium*, *Pleuridium*, *Bryum*; the abundant presence of liverworts with unevolved sporophytes and mosses with cleistocarpous capsules makes this flora very peculiar, different from the typical Mediterranean bryoflora.

Some literature data on the bryophyte flora of the Mediterranean temporary ponds are known. For Italy, we quote the papers on this peculiar bryological flora of Sardinia (Cogoni et al. 2004, 2006, 2016), a comparative study of the bryophytes in some Sardinian and Corsican wetlands (Cogoni et al. 2009) and a brief note on the temporary ponds of Apulia (Aleffi et al. 2009). For other Mediterranean countries, some significant papers on the Iberian Peninsula, Menorca and France are reported (e.g. Casas et al. 1998; Mandin & Hugonnot 2001; Grillas et al. 2004; Hugonnot 2004; Pericàs et al. 2009;

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etc.). Conversely, the information on the bryophyte vegetation is very scarce and fragmentary (Puglisi, Privitera, et al. 2015) despite its important application in the environmental field. In fact, the qualitative–quantitative analysis of the plant communities has a great significance in the environmental studies, well expressing the habitat–plant relationship. In this regard, a detailed analysis of the ecological and biological characters of the bryophyte communities of the Mediterranean temporary ponds, surveyed in Italy, is carried out in this paper, aimed to define an adaptative pattern according to the peculiar habitat features and the plant responses to the environmental demands.

## Material and methods

The field work was carried out during many investigations regarding the bryophyte vegetation of Italy, during a long period ranging from 1995 to 2010. The data refer to some territories of the regions Lazio (central Italy), Campania (southern Italy), Sicily and Sardinia.

The phytosociological relevés (Puglisi, Privitera, et al. 2015) here are used for the bio-ecological analysis by the life form, life strategy, lifespan, reproduction – sexual and asexual effort, spore size and dispersal strategy. The bryophyte communities analyzed are *Riccietum gougetianae* Marstaller 1993, *Riccietum canaliculatae* Puglisi & Privitera 2015, *Riccio sorocarpae-Funarietum fascicularis* Lecointe 1978 subass. *fossombronietosum* Lecointe 1978, of the phytosociological class *Barbuletea unguiculatae* Mohan 1978, *Pleuridio acuminati-Archidietum alternifolii* Puglisi & Privitera 2015 belonging to the class *Cladonio digitatae-Lepidozietea reptantis* Ježek & Vondrácek 1962, *Ricciocarpetum natantis* Segal 1963 em. Tüxen 1974 of the class *Lemnetea minoris* O. Bolòs & Masclans 1955.

The life forms follow the concept of Mägdefrau (1982). The term refers to the general appearance of a colony of bryophytes arising from the growth model, the branching pattern and general assemblage of individuals, influenced by environment. The classification is drawn from Hill et al. (2007), which recognizes the following categories: Solitary creeping, Solitary thalloid, Turf protonemal, Turf scattered, Thread and Lemnoid, with shoots not organized in colony, Turf, Tuft, Cushion, Dendroid, Mat rough, Mat smooth, Mat thalloid, Weft, Fan, Aquatic trailing and Aquatic colonial, with shoots organized in colony.

The life strategies follow the concept of During (1979), Frey and Kürschner (1991), and Kürschner and Frey (2013). Life strategy, based on the reproduction and dispersal strategies, reflects the ecological site conditions and gives knowledge on the mechanisms of habitat maintenance, establishment and re-establishment of species and communities (Puglisi et al. 2013a, 2013b, 2014; etc.). The life strategies are taken from Kürschner and Parolly (1999), Kürschner (2004), and Puglisi et al. (2012). They are: Fugitive, Annual shuttle, Short-lived shuttle, Perennial shuttle, Colonist, Perennial stayers, the last three further subdivided depending on the sexual and/or asexual reproduction effort.

The lifespan, sexual and asexual reproduction and spore size are mostly drawn from Hill et al. (2007). The estimate of the sexual reproduction is deduced from the information regarding the sporophyte frequency.

For each species and category, the mean percentage cover (MPC) values of the biological and ecological parameters within the community are calculated, based on the cover values (Frey & Kürschner 1991; Kürschner 2002, 2003, 2004; Puglisi et al. 2012; Puglisi, Kürschner, et al. 2015; etc.).

The frequency of the *taxa* in each community is reported according to the following scale: I: 1–20%; II: 21–40%; III: 41–60%; IV: 61–80%; V: 81–100%.

The nomenclature of the taxa follows Ros et al. (2007) for liverworts and hornworts and Ros et al. (2013) for mosses; the nomenclature of the syntaxa follows Marstaller (2006) and Puglisi and Privitera (2012). The *exsiccata* are kept in the Herbarium of the Department of the University of Catania (CAT).

## Results

The investigation on the bryophyte vegetation of the Mediterranean temporary ponds has highlighted the occurrence of several communities mostly diversified for their water requirements (Puglisi, Privitera, et al. 2015). They are ephemeral communities, occurring in substrate depressions subject to different periodic cycles of flooding and drought. They depend on the type of substrate beneath the pond, the depth of water, the duration of flooding and tolerate a more or less strong anthropic disturbance.

These communities are discussed below; the frequency of the species is reported in Table I, the analyzed characters in Table II.

***Riccietum gougetianae*** Marstaller 1993

It is a widespread community in the Mediterranean temporary ponds, found on moist soil of some ponds of Lazio, Sardinia and Sicily, which is often associated with the presence of *Isoëtes histrix* Bory. Ecologically, this communitiy behaves as a thermophytic, mesohygrophytic, ephemeral association. The strongly prevailing life form is the solitary thalloid (84.8%, Figure 1), due to the abundant presence of the species of the genus *Riccia*, such as *R. gougetiana*,

Table I. Frequency of the species in the bryophyte communities of the Mediterranean temporary ponds in Italy.

| Species | Bryophyte community | | | | |
|---|---|---|---|---|---|
| | Riccietum gougetianae | Riccietum canaliculatae | Riccio sorocarpae-Funarietum fascicularis fossombronietosum | Pleuridio acuminati-Archidietum alternifolii | Ricciocarpetum natantis |
| *Archidium alternifolium* | . | I | . | V | . |
| *Bryum dichotomum* | III | . | 1 | . | . |
| *Bryum radiculosum* | II | . | 1 | . | . |
| *Cephaloziella stellulifera* | . | . | . | I | . |
| *Cephaloziella turneri* | . | . | . | II | . |
| *Corsinia coriandrina* | III | . | . | . | . |
| *Dialytrichia mucronata* | . | . | . | . | II |
| *Drepanocladus aduncus* | . | . | . | . | V |
| *Entosthodon attenuatus* | . | . | . | II | . |
| *Entosthodon fascicularis* | . | . | III | . | . |
| *Epipterygium tozeri* | . | . | . | V | . |
| *Fossombronia angulosa* | . | . | . | III | . |
| *Fossombronia pusilla* | . | . | V | . | . |
| *Fossombronia caespitiformis* subsp. *caespitiformis* | II | . | . | . | . |
| *Fossombronia caespitiformis* subsp. *multispira* | III | IV | V | . | . |
| *Hedwigia stellata* | I | . | . | . | . |
| *Imbribryum alpinum* | . | III | . | . | . |
| *Oxymitra incrassata* | . | . | I | . | . |
| *Phaeoceros laevis* | . | . | III | I | . |
| *Plagiomnium elatum* | . | . | . | I | . |
| *Pleuridium acuminatum* | . | . | III | IV | . |
| *Ptychostomum pseudotriquetrum* | . | II | . | . | . |
| *Riccia beyrichiana* | . | . | . | I | . |
| *Riccia canaliculata* | . | V | . | . | . |
| *Riccia glauca* var. *glauca* | III | II | 1 I | . | . |
| *Riccia gougetiana* | V | IV | . | . | . |
| *Riccia michelii* | II | . | III | I | . |
| *Riccia nigrella* | II | . | IV | . | . |
| *Riccia sorocarpa* var. *sorocarpa* | III | II | V | . | . |
| *Ricciocarpos natans* | . | . | . | . | V |
| *Scapania compacta* | . | . | . | II | . |
| *Trichostomum brachydontium* | . | III | . | II | . |

*R. sorocarpa* var. *sorocarpa*, *R. nigrella*, *R. michelii*. The incidence of the other life forms is very low (turf 5.7%, solitary creeping 5.6%, mat thalloid 3.7% and mat rough 0.2%). The analysis of the life strategies has emphasized a very high occurrence of the shuttle species (overall value 94.3%, with annual shuttle 76.0%, short-lived shuttle 14.6%, perennial shuttle 3.7%; Figure 2), largely due to the dominance of the *Riccia* spp. and other liverworts, such as *Corsinia coriandrina*, *Fossombronia caespitiformis* subsp. *caespitiformis* and *F. caespitiformis* subsp. *multispira*. The sexual reproduction is common (96.3%, Table III), strongly related to the seasonal aspects with, in the annual species, immediate sporophyte formation and spore germination. The very large spores (up to 200 µm in diameter in *Riccia gougetiana*) provide chance dispersal (short-range dispersal), allowing the habitat re-establishment. The asexual reproduction is scarce, due only to the sporadic presence of *Bryum dichotomum* and *B. radiculosum*.

***Riccietum canaliculatae*** Puglisi & Privitera 2015

It is one of the most typical bryophyte communities of the Mediterranean ponds, occupying the banks which are wet or sometimes flooded. It is frequently related to the occurrence of *Isoëtes longissima* Bory. From an ecological point of view, it can be considered as a terricolous, meso-thermophytic, hygro-hydrophytic, ephemeral community. The finding sites are located in the Lazio region and in Sardina. In the *Riccietum gougetianae*, the life form solitary thalloid prevails (71.0%, Figure 1), due to the high occurrence of the *Riccia* spp., with *R. canaliculata* dominant. The other life forms are: turf (19.6%), represented by the acrocarpous mosses *Trichostomun brachydontium*, *Imbribryum alpinum*, *Ptychostomun pseudotriquetrum*, and solitary creeping (9.4%) with *Fossombronia* spp. Also in this community, the shuttle life strategy markedly prevails (overall value 85.2%, with annual shuttle 68.5% and short-lived shuttle 16.7%, Figure 2) for the predominance of species of the genera *Riccia* and *Fossombronia*. The colonist strategy is represented by the incidence of the acrocarpous moss *Imbrybryum alpinum* (10.3%) and the perennial stayer by *Ptychostomum pseudotriquetrum* (4.5%). Concerning the reproductive strategy, sexual reproduction is very frequent (95.3%) and the large spores, occurring in the soil bank, allow the habitat re-establishment for years, following the typical alternation of flooding/drought of the ponds.

Table II. Life forms, life cycle, sexual and asexual reproduction, spores size, dispersal strategy and life strategies of the taxa of the bryophyte communities of the Mediterranean temporary ponds in Italy.

| | Life form | Life cycle | Sexual reproduction | Spores (Ø in µm) | Asexual reproduction | Dispersal strategy | Life strategy |
|---|---|---|---|---|---|---|---|
| Anthocerotae | | | | | | | |
| *Phaeoceros laevis* (L.) Prosk. | Mt | a | fr | 30–46 | tub | sr | Pe |
| Hepaticae | | | | | | | |
| *Cephaloziella stellulifera* (Taylor ex Spruce) Schiffn. | Ms | p | fr | 9–12 | gem | sr,lr | Bg |
| *Cephaloziella turneri* (Hook.) Müll. Frib. | Ms | p | fr | uk | gem | sr,lr | Bg |
| *Corsinia coriandrina* (Spreng.) Lindb. | Mt | p | fr | 100–140 | thf | sr | Pk |
| *Fossombronia angulosa* (Dicks.) Raddi | Ms | a(p) | fr | 34–52 | a/r | sr | Pe |
| *Fossombronia caespitiformis* De Not. ex Rabenh. subsp. *caespitiformis* | Sc | a | fr | 34–41 | a/r | sr | Pe |
| *Fossombronia caespitiformis* subsp. *multispira* (Schiffn.) J.R. Bray and D.C. Cargill in Stotler et al. | Sc | p | ab | 42–56 | a/r | sr | Pk |
| *Fossombronia pusilla* (L.) Nees | Sc | a(p) | ab | 38–56 | a/r | sr | Pk |
| *Oxymitra incrassata* (Brot.) Sérgio & Sim-Sim | Mt | p | | 100–150 | a/r | sr | Pg |
| *Riccia beyrichiana* Hampe ex Lehm. | St | p | ab | 90–130 | a/r | sr | Pk |
| *Riccia canaliculata* Hoffm. | St | a | fr | 75–95 | a/r | sr | Pe |
| *Riccia glauca* L. var. *glauca* | St | a | ab | 70–100 | a/r | sr | Pe |
| *Riccia gougetiana* Durieu & Mont. | St | a | fr | 150–200 | a/r | sr | Pe |
| *Riccia michelii* Raddi | St | p | fr | 90–115 | a/r | sr | Pk |
| *Riccia nigrella* DC. | St | p | ab | 56–80 | a/r | sr | Pg |
| *Riccia sorocarpa* Bisch. var. *sorocarpa* | St | p | ab | 75–120 | a/r | sr | Pk |
| *Ricciocarpos natans* (L.) Corda | Le | a(p) | fr | 42–56 | a/r | sr | Pe |
| *Scapania compacta* (A. Roth) Dumort. | Mr | p | fr | 16–21 | gem | sr,lr | Av,g |
| Musci | | | | | | | |
| *Archidium alternifolium* (Hedw.) Mitt. | Tf | p | fr | 127–310 | tub | sr | Pk |
| *Bryum dichotomum* Hedw. | Tf | p | o | 8–16 | tub, bul | sr,lr | Bv,g |
| *Bryum radiculosum* Brid. | Tf | p | fr | 10–14 | tub | sr,lr | Bv |
| *Dialytrichia mucronata* (Brid.) Broth. | Tf | p | o | 14–16 | a/r | sr,lr | Ap |
| *Drepanocladus aduncus* (Hedw.) Warnst. | Ac | p | r | 16–16 | a/r | sr,lr | Ap |
| *Entosthodon attenuatus* (Dicks.) Bryhn | Ts | a | ab | 24–30 | a/r | sr | Pe |
| *Entosthodon fascicularis* (Hedw.) Müll. Hal. | Tf | a | fr | 24–28 | a/r | sr | Pe |
| *Epipterygium tozeri* (Grev.) Lindb. | Ts | p | r | 14–20 | tub, bul | sr,lr | Bv |
| *Hedwigia stellata* Hedenäs | Mr | p | fr | 23–30 | a/r | sr,lr | Pg |
| *Imbribryum alpinum* (Huds. ex With.) N. Pedersen | Tf | p | r | 12–14 | tub | sr,lr | Bv |
| *Plagiomnium elatum* (Bruch & Schimp.) T. J. Kop. | Tf | p | o | 17–25 | a/r | sr,lr | Pp |
| *Pleuridium acuminatum* Lindb. | Tf | a | ab | 25–30 | a/r | sr | Pe |
| *Ptychostomum pseudotriquetrum* (Hedw.) J. R. Spence & H. P. Ramsay | Tf | p | o | 12–25 | gem | sr,lr | Av,g |
| *Trichostomum brachydontium* Bruch | Tf | p | r | 14–18 | a/r | sr | Pk |

Abbreviations. a: ephemeral/annual; *ab*: abundant; Ac: Aquatic, colonial; Ag: perennial stayers with high sexual reproductive effort; Ap: perennial stayers with low sexual and asexual reproductive effort; a/r: absent-/rare; Av,g: perennial stayers with high sexual and asexual reproductive effort; Bg: colonist with sexual reproductive effort; Bv: colonist with asexual reproductive effort; Bv,g: colonist with high sexual and asexual reproductive effort; bul: bulbils; fr: frequent; gem: gemmae; Le: Lemnoid; lr: long-range; Mr: mat, rough; Ms: mat, smooth; Mt: Mat thalloid; o: occasional; p: pauciennial/perennial; Pe: annual shuttle; Pk: short-lived shuttle; Pg: perennial shuttle species with high sexual reproductive effort; Pp: perennial shuttle with moderate or rare sexual and asexual reproductive effort; r: rare; Rhg: rhizoid gemmae; Sc: solitary creeping; Sr: short-range; St: Solitary thalloid; Tf: turf; Thf: thallus fragmentation; Ts: turf, scattered; Tub: tubers; uk: unknown.

***Riccio sorocarpae-Funarietum fascicularis*** Lecointe 1978 subass. ***fossombronietosum*** Lecointe 1978

This subneutrophytic, mesophytic community is found in Sicily on moist soil at the outer margins of small, shallow ponds dried up in spring. It is one of the communities with fewer needs in water and most affected by human disturbance, behaving as mesophytic and euhemerobous. In this community, the species with solitary creeping life form (*Fossombronia* spp.) prevail (52.4%), followed by the solitary thalloid (22.5%) and turf (22.0%) (Figure 1). The strongly dominant life strategy is again the shuttle (overall value 92.2%, with short-lived shuttle 69.4%, annual shuttle 17.2%, perennial shuttle 5.6%, Figure 2), pointing out the predictable reappearance of the community in the same habitat. The other strategies are of minor or no significant value. The sexual reproduction is very frequent (94.7%, Table III) and the spores are very large, especially in *Riccia sorocarpa* (75–120 µm in diameter); the asexual reproduction effort is very scarce.

***Pleuridio acuminati-Archidietum alternifolii*** Puglisi & Privitera 2015

This community was recognized in shallow ponds, usually together with *Isoëtes durieui* Bory. It is the most widespread community, occurring in Lazio, Campania, Sardinia and Sicily. As regards the ecological exigencies, the community prefers open, acid soil which is damp or temporarily flooded. On the whole, it behaves as a terricolous, acidophytic, hygrophytic ephemeral community. This community is characterized by a high occurrence of acrocarpous mosses with turf and turf-scattered life forms (69.2

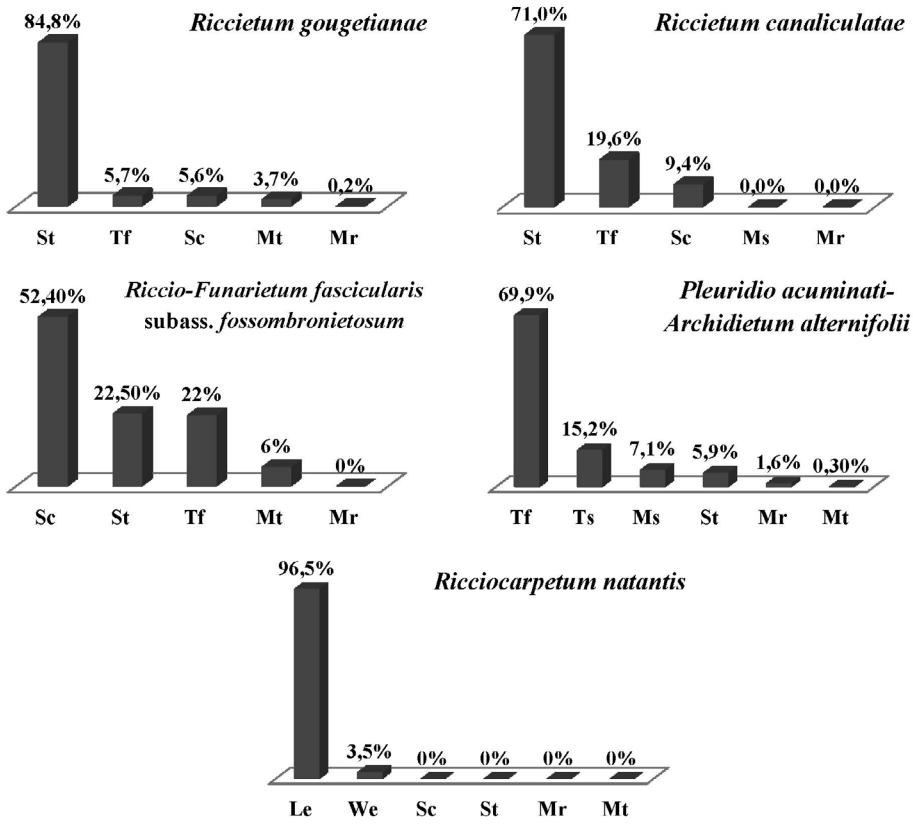


Figure 1. Incidence of the life forms (MPC values in %) in each bryophyte community of the Mediterranean temporary ponds in Italy. For abbreviations see Table II.

and 15.2% respectively, Figure 1), with *Archidium alternifolium*, *Pleuridium acuminatum*, *Epipterygium tozeri* as prevailing species. In the life strategies, the shuttle strategy is dominant (overall value 80.3%, with short-lived shuttle 61.4% and annual shuttle 18.9%, Figure 2). Here, the very large spores and achorous strategy is mostly due to the moss *Archidium alternifolium*, producing very few spores for capsule (4–28) with very large size (up to 310 μm in diameter). Moreover, *Archidium alternifolium*, as well as *Pleuridium acuminatum*, has an immersed, cleistocarpous capsule, with very short or lacking seta; therefore, in these conditions, the spores did not discharge easily, remaining in close proximity of the mother plant. The sexual reproduction effort is high (84.8%, Table III), with frequent production of capsules. The asexual reproduction is scarcely significant.

***Ricciocarpetum natantis*** Segal 1963 em. Tüxen 1974

This bryo-chormophytic community was found floating within the pool "Piscina della Verdesca", a seasonally flooded depression within the Circeo National Park (Lazio). It is floristically very poor, being constituted only by *Ricciocarpos natans*, a small liverwort floating on still waters, accompanied by two species of *Lemna*, free-floating aquatic flowering plants, and the hygro-hydrophytic pleurocarpous mosses *Drepanocladus aduncus* and *Dialytrichia mucronata*. Since the floating species dominate in this community, the lemnoid life form is obviously, strongly dominant (95.1%, Figure 1). The sexual and asexual reproduction effort is very low and the life strategy is the annual shuttle (95.1%, Figure 2).

## Discussion

### *Life form analysis*

The bio-ecological analysis of the bryophyte communities emphasizes that the most typical life form is the solitary thalloid, strongly prevailing in the *Riccietum gougetianae* (84.8%) and *Riccietum canaliculatae* (71.0%) (Figure 1), for the abundance of riccioid liverworts mostly diffused in mesic or moist sites. The biotype turf dominates in the *Pleuridio acuminati-Archidietum alternifolii* (69.9%) for the abundant occurrence of acrocarpous, caespitose mosses which are more drought-tolerant. The biotype solitary

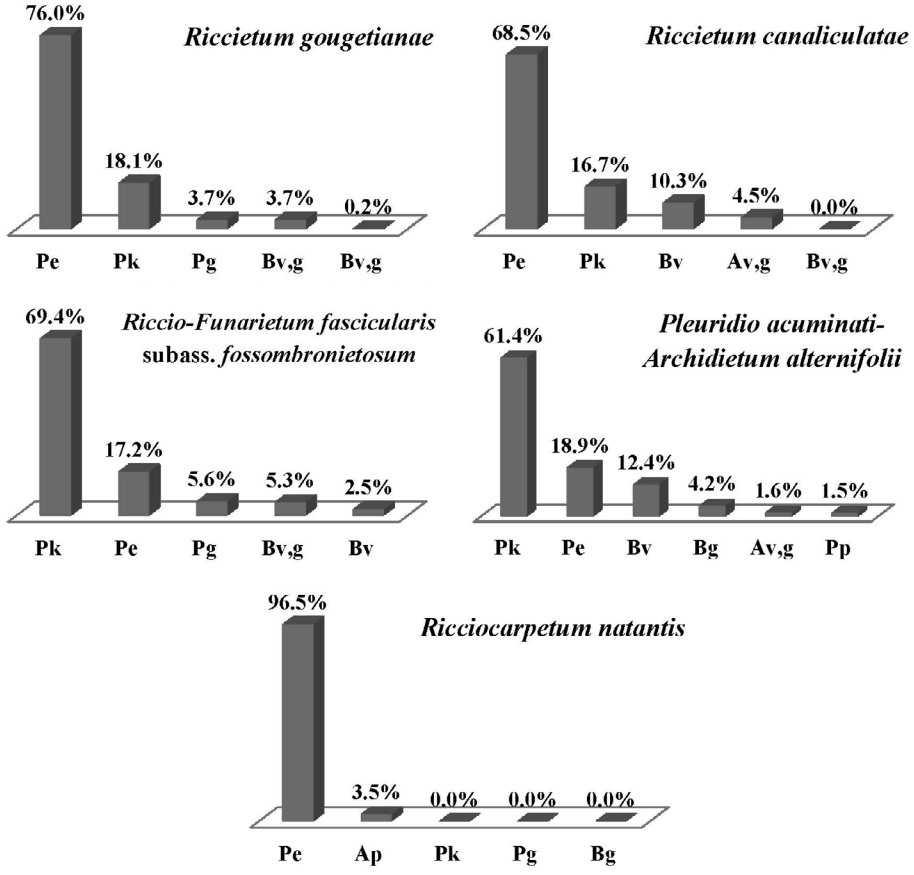


Figure 2. Incidence of the life strategies (MPC values in %) in each bryophyte community of the Mediterranean temporary ponds in Italy. For abbreviations see Table II.

Table III. Life syndrome in the bryophyte communities of the Mediterranean temporary ponds (MPC values in %); in bold the characters of the pattern. For the abbreviations see Table II.

| Bryophyte community | | Riccietum gougetianae | Riccietum canaliculatae | Riccio sorocarpae-Funarietum fascicularis fossombronietosum | Pleuridio acuminati-Archidietum alternifoliium | Ricciocarpetum natantis |
|---|---|---|---|---|---|---|
| Life form | **St, Sc** | **90.4** | **80.4** | **74.9** | 5.9 | – |
| | Tf, Ts | 5.7 | 19.6 | 22.0 | **85.1** | 2.2 |
| | Mr, Ms, Mt | 3.9 | – | 3.1 | 9.0 | – |
| | Le | – | – | – | – | 95.1 |
| | Ac | – | – | – | – | 2.7 |
| Life strategy | **Pe, Pk** | **90.6** | **85.2** | **86.6** | **80.3** | **95.1** |
| | Pg, Pp | 3.7 | – | 5.6 | 1.5 | – |
| | Bg, Bv, Bv,g | 5.7 | 10.3 | 7.8 | 16.6 | – |
| | Ap, Av,g | – | 4.5 | – | 1.6 | 4.9 |
| Spore size | **Large** (>25 µm in diameter) | **94.2** | **80.6** | **92.2** | **79.8** | **95.1** |
| | Small (<25 µm in diameter) | 5.8 | 19.4 | 7.8 | 20.2 | 4.9 |
| Life span | **a** | **76.0** | **73.0** | **66.6** | 20.1 | **95.1** |
| | p | 24.0 | 27.0 | 33.4 | 79.9 | 4.9 |
| Sexual reproduction effort | **High** | **96.3** | **95.3** | **94.7** | **84.8** | **95.1** |
| | Low | 3.7 | 4.7 | 5.3 | 15.2 | 4.9 |
| Dispersal strategy | **sr** | **94** | **85.2** | **92.2** | **81.8** | **95.1** |
| | sr/lr | 6.0 | 14.8 | 7.8 | 18.2 | 4.9 |

creeping, typical of the *Fossombronia* spp., prevails in the subassociation *fossombronietosum* of the *Riccio sorocarpae-Funarietum fascicularis* (52.4%), while the lemnoid biotype, typically linked to water, characterizes the floating association *Ricciocarpetum natantis* (95.1%).

*Life syndrome analysis*

The analysis of the life strategies emphasizes the very strong prevalence of the shuttle species, almost exclusively annual and short-lived, which, in each community exceed 80% (Figure 1). The life cycle of the shuttle species is strongly determined in the temporary ponds by seasonal fluctuations, strong alternation between dry and moist seasons and a severe stress period which is avoided by the bryophytes being present in the spore stage. In these species, the vegetation period is short, cyclic and starts predictably. The shuttle species produce large spores (>25 μm in diameter), strongly increasing short-range dispersion (engychory), and the capsules are often cleistocarpous, such as in *Archidium alternifolium* and *Pleuridium acuminatum*, or enclosed in the thallus, as in *Riccia* spp. (spores released by decay of thallus tissue), suggesting, in both cases, an achorous dispersal strategy (Kürschner & Parolly 1999). Species following this strategy survive by the large spores which are present in a diaspore bank; new plants establish immediately near the mother plant, thus lowering the risk of extinction by long range dispersal. Therefore, the dispersal capacity is low, mostly consisting in short-range dispersal or achory. The sexual reproduction is frequent, whereas the asexual (mostly tubers or gemmae) is rare or absent.

On the basis of the different strategies (avoidance vs. tolerance strategy of the gametophyte), it is possible to distinguish annual, short-lived and perennial shuttle species. The annual shuttle species combine short-lived gametophytes with immediate sporophyte formation and spore germination; in the Mediterranean temporary ponds, the most diffused annual shuttle species are *Riccia gougetiana*, *R. canaliculata*, *R. glauca*, *Ricciocarpos natans*, *Pleuridium acuminatum* (Table I). The short-lived shuttle species combine a more long-lived gametophytes (pauciannual, however not perennial) and, as well as the annual species, the production of large spores. In the investigated habitat, *Archidium alternifolium*, *Riccia sorocarpa*, *R. michelii*, *Fossombronia caespitiformis* subsp. *multispira*, belonging to this functional type, are the most widespread (Table I). Instead, the perennial shuttle species, characterized by a long-lived, pluriannual gamethophyte, are rare in this habitat. On the whole, the annual shuttle species prevail in the *Riccietum gougetianae* (76.0%), *Riccietum canaliculatae* (68.5%) and *Ricciocarpetum natantis* (96.5%), the short-lived shuttle species prevail in the *Pleuridio acuminati-Archidietum alternifolii* (61.4%) and *Riccio sorocarpae-Funarietum fascicularis* subass. *fossombronietosum* (69.4%).

Another category of life strategy, occurring in all the communities but with low values, is represented by the colonist species which have a moderately short lifespan and occur in habitat unpredictable disappearing. These species are characterized by a moderately short lifespan of only few years (pauciannual), a high sexual reproduction effort with the production of numerous, small spores which often allow long-range dispersal. The asexual reproduction is frequent by rhizoid gemmae, leaf gemmae, tubers, allowing a rapid establishment of the populations. *Cephaloziella stellulifera*, *C. turneri*, *Bryum dichotomum*, and *B. radiculosum* are typical examples of colonist species. The highest values of the colonist species are found in the *Pleuridio acuminati-Archidietum alternifolii* (overall value 16.6%: 12.4% with asexual reproduction effort, 4.2% with sexual reproduction effort) and *Riccietum canaliculatae* (10.3%).

The incidence of the species with functional type perennial stayers is negligible. They are perennial species, often with low sexual and asexual reproduction effort; the spores are numerous and small, providing chance dispersal. These species are typically frequent in late successional stages or long-lasting habitats under more or less constant environmental conditions. In the investigated habitat, this strategy is represented only by *Ptychostomum pseudotriquetrum*, *Scapania compacta* and *Drepanocladus aduncus*, which is very rare in the bryophyte vegetation of the temporary ponds (Table I).

## Conclusion

The life syndrome analysis of the bryophyte communities of the Mediterranean temporary ponds has emphasized a set of common adaptative characters linked to the peculiarity of the habitat (Table III). These communities, even if colonizing different sites or microsites, share many strategies regarding lifespan, spore size, sexual reproduction, spore dispersal and life strategy. This suggests an adaptative pattern within species of unrelated taxa, which evolve, by parallel evolution, under similar environmental pressure independently from their taxonomical and phylogenetic relationships. The coevolved adaptative characters allow a successful establishment and ensure habitat maintenance of the communities.

Considering the conditions of the investigated habitat, characterized by periodic cycles of flooding and droughts, the communities dominated by shuttle species, annual and short-lived shuttle, result strongly winner, showing competitive advantages. The strong occurrence and abundance of the shuttle species distinguishes this peculiar habitat, unlike many other Mediterranean habitats normally characterized by colonist species, reproducing by small spores and colonizing habitat with an unpredictable start. In the bryophyte communities of the ponds, the shuttle species show a solitary thalloid or solitary creeping dominant life form in the liverwort set or turf life form in the acrocarpous mosses.

Other coevolved adaptative characters are the short lifespan (annual or pauciannual), high sexual reproduction effort, large spores (up to 310 μm in diameter) and drought-tolerance. In particular, the drought-tolerance is mostly provided by the avoidance strategy due to the high occurrence of the annual species (Table III). Particular importance is given by the achorous strategy, with large spores produced within a cleistocarpous capsule (*Archidium alternifolium*, *Pleuridium acuminatum*) or immersed in the thallus (*Riccia* spp.), thus increasing strongly the potential of short-range dispersal (Table III). These spores remain in the soil bank, ensuring the survival in the unfavorable period and lowering the risk of local extinction of the species; this is particularly important for the temporary ponds which dry down after the winter floods. The individuated strategies allow the establishment, re-establishment and habitat maintenance of the species, populations and communities.

In conclusion, from the analyses of the life syndromes of the bryophyte communities emerges an adaptative pattern corresponding to a functional type related with the habitat conditions. It is characterized by species with annual and short-lived shuttle life strategy, short lifespan, very large spores, short-range dispersal, solitary thalloid, solitary creeping or turf life forms and high sexual reproduction effort. The pattern is linked to a predictable, cyclic, temporary habitat, as that of the Mediterranean temporary ponds.

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## References

Aleffi M, Ernandes P, Zuccarello V. 2009. La componente briofitica degli stagni temporanei mediterranei in Puglia. Atti 109° Congresso della Società Botanica Italiana [The bryophyte component of the Mediterranean temporary ponds in Apulia]. 158.

Bagella S, Caria MC. 2012. Diversity and ecological characteristics of vascular flora in Mediterranean temporary pools. C R Biol 335: 69–76.

Bagella S, Caria MC, Filigheddu R. 2013. Gap analysis revealed a low efficiency of Natura 2000 network for the conservation of endemic species in Mediterranean temporary freshwater habitats. Plant Biosyst 147: 1092–1094.

Caria MC, Capra GF, Buondonno A, Seddaiu G, Vacca S, Bagella S. 2015. Small-scale patterns of plant functional types and soil features within Mediterranean temporary ponds. Plant Biosyst 149: 384–394.

Casas C, Cros RM, Brugués M, Sérgio C, Font J. 1998. Els briòfits de les basses de l'Albera, Alt Empordà [The bryophytes of the ponds of Albera, Alt Emporda]. Butll Inst Catalana Hist Nat 66: 73–80.

Cogoni A, Filippino G, Marignani M. 2016. Small-scale pattern of bryoflora in Mediterranean temporary ponds: hints for monitoring. Hydrobiologia. http://dx.doi.org/10.1007/s10750-015-2635-0 [online version].

Cogoni A, Flore F, Adamo C, Lai R, Scrugli A. 2006. Ecology of bryophytes of damp areas at "Giara di Gesturi" (Southern Central Sardinia). Bocconea 19: 65–76.

Cogoni A, Flore F, Adamo C, Scrugli A. 2004. Bryological flora of the Giara di Gesturi tableland (Southern Central Sardinia). Braun-Blanquetia 34: 51–58.

Cogoni A, Scrugli A, Cortis P. 2009. Bryophyte flora of some temporary pools in Sardinia and Corsica. Plant Biosyst 143: S97–S103.

During HJ. 1979. Life strategies of bryophytes: A preliminary review. Lindbergia 5: 2–18.

Frey W, Kürschner H. 1991. Lebensstrategien von terrestrischen Bryophyten in der Judäischen Wüste [Life strategies of terrestrial bryophytes in the Judean Desert]. Botanica Acta 104: 172–182.

Grillas P, Gauthier P, Yavercovski N, Perennou C. 2004. Les mares temporaires méditerranéennes. Volume 2 Fiches espèces [The Mediterranean temporary ponds. Volume 2. Species information sheets]. Station biologique de la Tour du Valat, Arles (France).

Hill MO, Preston CD, Bosanquet SDS, Roy DB. 2007. BRYOATT: Attributes of British and Irish Mosses, Liverworts and Hornworts. Cambridge: Centre for Ecology and Hydrology.

Hugonnot V. 2004. Contribution à la chorologie et à l'écologie des Ricciacées du Massif Central (France), principalement de l'Ardèche et de la Haute-Loire [Contribution to the chorology and ecology of the Ricciaceae of the Massif Central (France), mainly of Ardèche and Haute-Loire]. Cryptogamie Bryol 25: 39–67.

Kürschner H. 2002. Life strategies of Pannonian loess cliff bryophyte communities. Studies on the cryptogamic vegetation of loess cliffs, VIII. Nova Hedwigia 75: 307–318.

Kürschner H. 2003. The Riccietum jovet-astii – argenteolimbatae ass. nov. of the Jabal Arays area, Yemen – Life strategies of a remarkable xerotropical African bryophyte community. Nova Hedwigia 76: 399–413.

Kürschner H. 2004. Life strategies and adaptations in bryophytes from the Near and Middle East. Turk J Bot 28: 73–84.

Kürschner H, Frey W. 2013. Life strategies in bryophytes – A prime example for the evolution of functional types. Nova Hedwigia 96: 83–116.

Kürschner H, Parolly G. 1999. The Epipterygio-Riccietum frostii ass. nov.: Ecology and life strategies of an ephemeral bryophyte community in western Turkey. Lindbergia 24: 84–92.

Mägdefrau K. 1982. Life forms of Bryophytes. In: Smith AJE, editor. Bryophyte ecology. London: Chapman & Hall. pp. 45–58.

Mandin J-P, Hugonnot V. 2001. Présence de mares temporaires méditerranéennes en Ardèche (France) [The occurrence of the Mediterranean temporary ponds in Ardèche (France)]. J Bot Soc Bot France 16: 61–70.

Marstaller R. 2006. Syntaxonomischer Konspekt der Moosgesellschaften Europas und angrenzender Gebiete [Syntaxonomical synopsis of the moss associations of Europe and adjacent areas]. Haussknechtia 13: 1–192.

Minissale P, Sciandrello S. 2016. Ecological features affect patterns of plant communities in Mediterranean temporary rock pools. Plant Biosyst 150: 171–179. http://dx.doi.org/10.1080/11263504.2014.986248.

Pericàs J, Rosselló JA, Mascaró J, Fraga P. 2009. The importance of bryophytes in the Mediterranean temporary ponds of Minorca. In: Fraga i Arguimbau, P., editor. International Conference on Mediterranean Temporary Ponds. Proceedings & Abstracts. Consell Insular de Menorca. Recerca, 14. Maó, Menorca: 395.

Puglisi M, Costa R, Privitera M. 2012. Bryophyte coastal vegetation of the Cilento and Vallo di Diano National Park (S Italy) as a tool for ecosystem assessment. Plant Biosyst 146(Supplement): 309–323.

Puglisi M, Kürschner H, Privitera M. 2013a. Saxicolous bryophyte communities of mountain areas of Greece: Phytosociology, ecology, life forms and life strategies. Nova Hedwigia 97: 159–178.

Puglisi M, Kürschner H, Privitera M. 2013b. Syntaxonomy, life forms and life strategies of the bryophyte vegetation of the Carnic Alps (NE Italy). Nova Hedwigia 96: 325–349.

Puglisi M, Kürschner H, Privitera M. 2014. The bryophyte association *Solorino saccatae–Distichietum capillacei* Reimers 1940 on the Mediterranean mountains: A tool for evaluating natural and conservative environments. Plant Biosyst 148: 815–824.

Puglisi M, Kürschner H, Privitera M. 2015. The *Schistidio atrofusci-Grimmietum pulvinatae*, a new association of the class *Grimmietea anodontis* on the Mediterranean mountains. Nova Hedwigia 100(1–2): 205–214.

Puglisi M, Privitera M. 2012. A synopsis of the Italian bryophyte vegetation. Cryptogamie Bryol 33: 357–382.

Puglisi M, Privitera M, Minissale P, Sciandrello S. 2015. The bryophyte vegetation of the Mediterranean temporary ponds in Italy. Plant Sociology 52(2): 69–78.

Ros RM, Mazimpaka V, Abou-Salama U, Aleffi M, Blockeel TL, Brugués M, et al. 2007. Hepatics and Anthocerotes of the Mediterranean, an annotated checklist. Cryptogamie, Bryologie 28(4): 351–437.

Ros RM, Mazimpaka V, Abou-Salama U, Aleffi M, Blockeel TL, Brugués M, et al. 2013. Mosses of the Mediterranean, an annotated checklist. Cryptogamie, Bryol 34(2): 99–283.